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Protecting Ecosystems from Underground Invasions – Seed Bank Dynamics in a Semi-Arid Shrub-Steppe

David R. Clements¹ and Lynne B. Atwood²

¹Trinity Western University, Langley, British Columbia

²Genoa Environmental, Cobble Hill, BC
Canada

1. Introduction

Plant invasions threaten natural and managed ecosystems throughout the world (Hobbs & Humphries, 1995). Invasive plants reduce species diversity through competition with native plant species, leading to local reductions in populations of native species. According to E.O. Wilson: “on a global basis...the two great destroyers of biodiversity are, first habitat destruction and, second, invasion by exotic species” (Simberloff et al., 1997). In some cases invasive plants act more as “passengers” than “drivers” of ecological change in degraded ecosystems (MacDougall & Turkington, 2005). In either capacity invasive plants are a significant biotic element to consider in evaluating the integrity of a given type of ecosystem. The spread of non-native plants throughout the world has a homogenizing impact on regional floras, particularly given the tendency of certain invasive species in forming monocultures or near monocultures. Yet the seriousness of plant invasions is sometimes called into question (Larson, 2007) and because invasion biology is a relatively young field (Davis, 2009), further research is required to better assess the impacts of invasive species on ecosystem function.

Shrub-steppe ecosystems occur in North America in the rainshadow of the western mountain ranges. These habitats are characterized by relatively low precipitation and extremes of temperature with vegetation structure typified by scattered shrubs of various species such as *Artemisia* spp. (sagebrush) or *Purshia tridentata* (antelope-brush). Similar ecosystems are found throughout the world in high altitude temperate continental areas such as southwestern Russia, other parts of Asia, and South America. The South Okanagan Valley in British Columbia is representative of shrub-steppe ecosystems featuring *P. tridentata* prominently and is recognized federally as a biodiversity hot spot (Mosquin et al., 1995). Isolated remnant grasslands are home to Provincially and Federally listed endangered wildlife and form a key component of the South Okanagan Conservation Strategy (Bryan, 1996). A major contributor to the loss of biodiversity in these intermountain areas in British Columbia and throughout the Pacific Northwest of North America is the presence of extensive infestations of invasive species (Clements & Scott, 2011). Key invasive plants that degrade arid grasslands in this region include *Centaurea diffusa* (diffuse knapweed) and

Bromus tectorum (cheatgrass), which form large, spreading patches (Mack, 1981; Roché & Roché, 1999; Clements et al., 2007; Clements & Scott, 2011).

Restoration of such areas is a serious challenge; a long-history of grazing, invasion of non-native plants, other types of soil disturbance and habitat fragmentation in shrub-steppe habitats tends to simplify the ecosystem and reduce its integrity. Although Europeans arrived in the western U.S. decades earlier, it was during the 30 year period from the end of the U.S. civil war in 1865, that the steppe regions in western North America from British Columbia south to Nevada underwent a dramatic transformation from small isolated habitation by Europeans to the development of more permanent farmland and ranches (Meinig, 1968; Elliott, 1973). This resulted in the first serious weed invasion but many of the serious modern-day invaders such as *B. tectorum* did not arrive until around the turn of the 20th century, but quickly made up for lost time covering large areas of these interior grasslands by 1914 (Mack, 1981; Mack, 1986). The large scale movement and grazing of cattle, coupled with the introduction of horticultural crops such as apples and other fruit trees in the 20th century has continued to provide disturbed conditions conducive to the spread of non-native plants (Krannitz, 2008; Clements & Scott, 2011). The native grassland in this area is dominated by shrubs such as *P. tridentata* and perennial bunchgrasses such as *Pseudoroegneria spicata* (bluebunch wheatgrass) and others such as *Hesperostipa comata* (needle-and-thread grass) (Atwood & Scudder, 2003; Erickson, 2003). The soils may often be shallow and sandy, but in the absence of heavy grazing or other pronounced disturbances, a microbiotic crust, dominated by mosses and lichens, is maintained and provides valuable ecosystem services such as soil moisture retention (Loope & Gifford, 1972; Atwood & Krannitz, 2000).

A unique aspect of population dynamics in seed bearing plants is recruitment of populations over multiple time scales via seed banks. The invasive success of many non-native species is attributed to a persistent soil seed bank (Baker, 1974; Holm et al., 1977; Roché & Roché, 1999). Seed banks of invasive species can be both indicative of past disturbances and predictive of future weed population dynamics, and thus have great significance to restoration ecology, although there is considerable scope for further work in this area (Bakker et al., 1996). Many non-native invasive plants, particularly annuals, produce persistent seed banks and thus are very difficult to remove from an ecosystem once established, particularly if disturbances such as soil tillage (Clements et al., 1996), fire (Mandle et al., 2011) or grazing (Clements et al., 2007) occur regularly. Seed bank sizes and dynamics vary according to ecosystem type (Leck et al., 1989), and are dependent on climatic factors, disturbance regimes, edaphic conditions and plant community structure. Thus the seed bank dynamics must be understood in these particular contexts. Two invasive alien plant species of particular interest in this system as previously mentioned are *C. diffusa* and *B. tectorum*. Both of these exhibit seed banks in response to disturbance, with the seed bank of *C. diffusa* tending to be more persistent (Clements et al., 2007).

This chapter describes the results of a study examining various restoration treatments for the antelope brush ecosystem in the southern Okanagan and makes recommendations for the restoration of such systems. The objectives of the study, conducted from 1998-2003 were as follows:

1. measure temperatures under polyethylene sheets used in experimental solarization trials in the southern Okanagan,
2. evaluate survival of diffuse knapweed and seeds of other native and non-native species *in situ* within solarization treatments,
3. investigate effects of high temperatures on *Centaurea diffusa* (diffuse knapweed) and *Sporobolus cryptandrus* (sand dropseed) seed viability, using temperatures equivalent to those that would be experienced under solarization, and
4. evaluate an array of alternative restoration treatments involving control of non-native species or seeding of native species.

2. Study area

The study was conducted in a semi-desert shrub steppe ecosystem dominated by *Purshia tridentata* (antelope bitterbrush) in the southern, more arid section of the Okanagan Valley in British Columbia, Canada. This ecosystem occurs within the northernmost extension of the intermountain plateau which extends southward to Nevada. The southern Okanagan valley receives just over 300 mm of precipitation annually. Precipitation is bi-modal: early summer (June) and mid-winter (December – January) (Chilton 1988). The native bunchgrass community persists but is highly invaded by non-native grasses and forbs, particularly where heavy grazing has occurred (Atwood and Scudder, 2003; Clements et al., 2007; Krannitz, 2008). The soil is typically overlaid with a microbiotic crust comprised of a mixture of lichen, moss, liverworts, algae, fungi, and bacteria. Atwood and Krannitz (2000) found that five days after a rainfall event in this region, crusted soils retained an average of 31% of the initial soil water, while bare soils retained just 9.5%.

The research was conducted at the Osoyoos Desert Centre, a site located several km northwest of Osoyoos, British Columbia (Fig. 1). The Osoyoos Desert Society acquired 50-ha of shrub steppe with a *P. tridentata* system heavily invaded by non-native plants but still containing substantial native plant diversity. The *P. tridentata* shrub steppe is susceptible to livestock grazing, with heavy grazing resulting in reduction of native species and increased cover of invasive nonindigenous species (Krannitz, 2008). Historically, cattle grazed the Osoyoos Desert Centre site every year between March and June. Prior to the establishment of the Centre, about 40 cattle were removed from the site.



Fig. 1. Antelope brush (*Purshia tridentata*) landscape at the Osoyoos Desert Centre study site, near Osoyoos, British Columbia, Canada; photo courtesy of the Osoyoos Desert Centre

3. Research methods

In 1998, when the Osoyoos Desert Centre was established, plots were set up on the site in five replicates to examine the impact of various restoration treatments.

3.1 Restoration treatments

Six different restoration treatments were put in place utilizing 10 x 10 m plots at the Osoyoos Desert Centre site (Table 1).

Treatment	Year initiated
Solarization	1998
Native bunchgrass hayseeding	1998
Removal of livestock grazing (controls)	1998
Manual + chemical control of <i>Centaurea diffusa</i>	1999
Broadcast seeding of natural grasses	2000
Addition of native vesicular arbuscular mycorrhizae and native seed	2000

Table 1. Restoration treatments at the Osoyoos Desert Centre site, 1998-2003, showing treatment type and year initiated

3.1.1 Solarization

Solarization plots were randomly chosen from a subset of plots with a high percent cover of diffuse knapweed (two plots per replicate for a total of 10 plots). Solarization plots averaged 27± 12 SD% cover of diffuse knapweed. Polyethylene sheets were placed over the entire 10 × 10 m plot in 1998, and left in place for a minimum of two growing seasons. The plastic was removed from 5 of the plots in April 2000 (plastic removed from 1 plot per replicate). Vegetation data were collected from the plots before the plastic was put down and following its removal (June 2000 and 2002).

3.1.2 Native bunchgrass hayseeding

The hayseeding experiment was initiated on two plots per replication (10 plots total) in September 1998. As seed matured, seed heads and plant stalks were cut from four native bunchgrasses; *Aristida longiseta* (red three-awn), *Hesperostipa comata* (needle and thread grass), *Sporobolus cryptandrus* (sand dropseed), and *Pseudoroegneria spicata* (bluebunch wheatgrass). The plant material was collected from natural shrub-steppe communities within the South Okanagan Basin Ecoregion. Approximately 200 litres of plant material (50 litres from each species) was distributed evenly over each 100 m² plot.

3.1.3 Removal of livestock grazing (controls)

In 1998, two randomly chosen 100-m² plots in each replication were established as control plots (10 plots total). Species identity and percent cover data were collected annually, in June, from 1998 to 2002. The control plots were monitored to document changes in the plant community without livestock grazing or restoration activity.

3.1.4 Manual and chemical control of *Centaurea diffusa*

The manual control of *C. diffusa* experiment was to determine the most effective time to hand weed *C. diffusa*, and whether weed density was related to the timing of the manual control. The first hand pulling was scheduled for early May, after which monthly treatments were scheduled if weed density was greater than 25% of the original *C. diffusa* cover.

The experiment for the chemical control of *C. diffusa* was implemented in 2000. *C. diffusa* plants in two 100-m² plots per replication (10 plots) were spot sprayed with an over-the-counter broadleaf herbicide, Killex, at the recommended label rate of 1.85 kg active ingredient per hectare in May 2000. Killex, a combination of 2,4-D, mecoprop, and dicamba was used in the chemical control experiment to determine if adequate control of *C. diffusa* could be obtained using a less expensive broad-leaf herbicide with less residual than the commonly used Tordon 22K (picloram).

3.1.5 Addition of native vesicular arbuscular mycorrhizae and native seed

Five 100-m² plots were divided into four 25-m² subplots and two treatments (Nurse plant inoculant and Soil-Root inoculant) and two control plots (no inoculant) were randomly established in each plot. The experimental plots were tilled, inoculated or not then seeded with the native grass seed mix at 28 kg per ha. The experiments were installed in the fall of 2000 and percent cover data for the seeded native grasses were collected in June 2001 and 2002.

3.1.6 Broadcast seeding of natural grasses

Broadcast seeding experiments were initiated in October 2000. The 100-m² plots were double split, producing four 25-m² subplots. One-half of the plots were tilled to mimic soil disturbance that would be associated with development projects. Shrubs remained, but existing herbaceous vegetation was cut and removed from the plot before tilling and the soil was packed after tilling. Standing herbaceous vegetation was also cut and removed from the no-till plots. Non-native species remaining in the plots were spot treated with the herbicide glyphosate applied at the full label rate.

The seed mix consisted of four perennial native bunchgrasses (*Aristida longiseta*, *Hesperostipa comata*, *Sporobolus cryptandrus*, and *Pseudoroegneria spicata*) and one annual agronomic grass *Lolium multiflorum* (annual ryegrass). All native grass seed used in the mix was collected from the area immediately adjacent to the research site. The native grasses were combined evenly in the mix (25% live seed per species) and seed rates were 28 kg per ha (1027 seeds per m²) and 41 kg per ha (1504 seeds per m²). Application rates were adjusted to account for the germination rate of the collected seed. Each seed rate was broadcast on one-half of the 100-m² plot and the soil was rolled after seeding.

3.2 Above-ground plant population monitoring

Plant species identity and percent cover data for all vascular plant species were collected annually for each of the 10 × 10 m plots, in June, from 1998 to 2002. Soil texture data collected from the plots in 1998 identified differences in soil texture between the replications. Replicates 1-4 contained significantly more silt and significantly less sand than Replicate 5. As a result, for many of the experiments, data from Replicates 1 to 4 were analysed separately from data collected from Replicate 5.

3.3 Seed bank studies

A hand coring device was used to collect 2.3 × 10 cm soil cores. In May of 1999, three cores were randomly taken from each 10 × 10 m plot sampled and bulked, except in the case of the

solarization plots wherein the sampling procedure was repeated three times to obtain a larger sample of *C. diffusa* seeds (collecting a total of nine 2.3 × 10 cm cores from each plot).

Seeds were extracted from the soil using the soil flotation method (Malone, 1967). The soil was dispersed using an aqueous solution of sodium hexametaphosphate (50 g L⁻¹) and sodium bicarbonate (25 g L⁻¹). Magnesium sulfate (75 g L⁻¹) was added to the aqueous solution to extract the seeds by flotation. Each soil sample was mixed slowly with 400 ml of the chemical solution, and agitated for two minutes. The organic matter was decanted through a 1.25 mm sieve, with a finer 0.1 mm sieve below. Any seeds appearing on the 1.25 mm were collected. The solution was then re-mixed with the inorganic material to allow any remaining seeds to achieve flotation. This solution was then re-decanted twice more through the 0.1 mm sieve. The organic material trapped by the 0.1 mm sieve was placed to dry in a Petri dish for a minimum of one week before the seeds were counted.

Germination tests were done on seeds of the following species as they were extracted from the samples: *Sporobolus cryptandrus*, *Centaurea diffusa*, *Stipa comata* and *Bromus tectorum*. Seeds were placed into Petri dishes with a Whatcom filter paper and moistened with deionized water. The dishes were then placed in a growth chamber set at 14 hours light at 25°C and 10 hours dark at 15°C. After two weeks under these conditions, the germinated seeds were counted using a dissection microscope.

3.4 Experimental exposure of seeds to high temperatures

Temperatures within the solarization plots ranged as high as 78.0 C (Table 2). The maximum ambient temperature recorded was 39.9 C. The mean daily high temperature for the period when temperatures were recorded from July 27-Oct. 9 was 26.9 C.

Time period	Solarization temperatures			Ambient air temperatures	
	Highest Recorded	Mean daily max	# days above 40 C	Highest recorded	Mean daily max
August	75.1	64.3 (11.1)	28.4 (1.6)	39.9	30.8 (5.1)
September	62.5	52.9 (9.7)	21.2 (4.8)	30.88	24.3 (4.7)
July 27-October 9	78.0	57.3 (13.0)	56.2 (8.0)	39.9	26.9 (6.4)

Table 2. Temperatures (± standard deviation) at the soil surface under solarization compared to ambient air temperatures in 1999 at Osoyoos, British Columbia, Canada

The temperatures under solarization were marginally higher than temperatures of 60-70 C reported in Mississippi (Egley, 1983), 42-52 C recorded in Israel (Horowitz et al., 1983), and a 57 C maximum recorded in Syria (Linke, 1994). As indicated by the ambient temperatures, summer temperatures near 40 C are not uncommon in the southern Okanagan valley, and thus solarization treatments attain high temperatures. The peak temperatures usually occurred in early afternoon, but as the example readings from the first week of August indicate (Fig. 2), the duration of periods above 40 C frequently persisted at least 5 hours. On this basis, an experimental period of 5-h exposure was chosen for heat-shock experiments, along with a 1-h exposure for comparison.

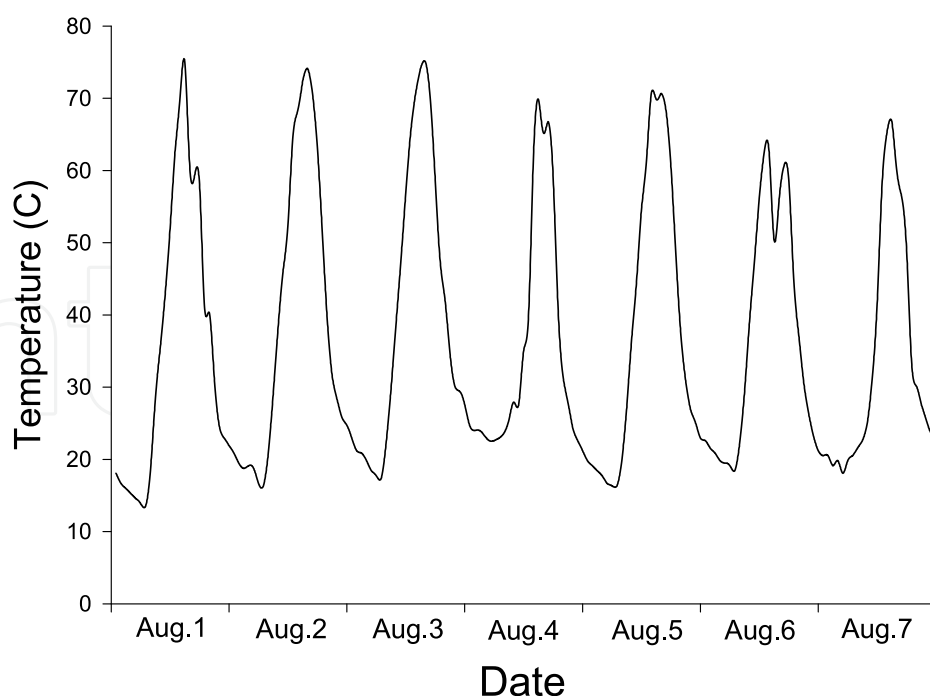


Fig. 2. A seven day sequence of hourly recorded temperatures within a solarization plot in the southern Okanagan valley of British Columbia, Canada (plot #507 which had the highest recorded temperatures)

Seeds of both the invasive alien species, *C. diffusa*, and the native species *S. cryptandrus* were tested for resilience to high temperatures that would be experienced under solarization treatments. Seeds for *C. diffusa* heat shock tests (Mangrich & Saltveit, 2000) were collected from the field in the fall and stored dry at room temperature prior to exposure to high temperatures in the laboratory. Seeds of *S. cryptandrus* for testing were randomly selected from the seed bank samples collected at the Osoyoos Desert Centre study site.

Seeds in Petri dishes were exposed to a given temperature for either 1 h or 5 h, with Petri dishes lined with dry or damp filter paper to signify dry or wet treatments, respectively. Temperatures tested for *C. diffusa* were 40, 50, 60, 70, 80, 90, and 100 C; temperatures tested for *S. cryptandrus* were 70 and 110 C. The 5 h period was to simulate the approximate duration of exposure to peak temperatures experienced daily under solarization in the field. After the high temperature exposure, seeds were removed from the oven and tested for germination (Fig. 3).

Seeds were tested for germination in a growth cabinet maintained at a day/night regime of 25 C/15 C, and a 14-h photoperiod, consistent with the germination requirements of diffuse knapweed (Nolan & Upadhyaya, 1988). Seeds were placed on moist filter paper. Protrusion of the radical by about 2 mm was the criterion for germination. After two weeks, ungerminated seeds were tested for viability using the tetrazolium method (Lakon, 1949; Van Waes & Debergh, 1986). A 1% 2, 3, 5-triphenyltetrazolium chloride (TTC) solution was made by dissolving 5 g of TTC in 500 ml of sterile distilled water. The pH was adjusted to 7 with 1 M NaOH. Seeds were dissected to expose the embryos and soaked in water prior to adding the tetrazolium solution. The embryo was evaluated for color change within 8 h.

White embryos that turned pink were recorded as viable. Seeds with embryos that failed to change color, or that were soft and showing signs of decay were evaluated as nonviable. In the case of seeds of *C. diffusa* exposed to 100 C, the embryos took on a distinctly different appearance, and thus the results for the tetrazolium test were not reported.



Fig. 3. Germinating seeds of *Sporobolus cryptandrus*; photo by Hannah Buschhaus

4. Restoration treatment results

More than 70 vascular plants were recorded in the above-ground communities in the Osoyoos Desert Centre plots during the 5-year study. Only 28 species were identified in the seed bank (Table 3), although several species in the seed bank were unidentified. This asymmetry between above-ground and seed bank communities is common to most ecosystems, including the antelope brush ecosystem (Clements et al., 2007).

The four dominant species in terms of density m^{-2} identified in the seed bank were *Sporobolus cryptandrus* (66-67% over the two sampling periods), *Centaurea diffusa* (10-14%), *Polygonum douglassii* (6-9%) and *Verbena bracteosa* (6%). This was similar to the pattern seen in another study which encompassed 10 sites in the southern Okanagan, but did not include the Osoyoos Desert Centre Site (Clements et al. 2007) with the exceptions that *B. tectorum* was more abundant at these other sites and *V. bracteosa* did not figure prominently. *Bromus tectorum* comprised 2% of the seed bank on average in the Osoyoos Desert Centre study; in the study spanning 10 sites *B. tectorum* seed comprised 21% of the seeds found in the seed bank (Clements et al. 2007).

Of these four dominant seed bank species, only *C. diffusa* was not native, and as long-term strategies for restoration of plant communities and associated ecosystems are developed, seed banking native species such as *S. cryptandrus*, *P. douglassii*, and *V. bracteosa* can be valuable facets of such a strategy, and represent significant potential species for seeding (Clements et al., 2007).

Species	Density m ⁻² in 1999	Density m ⁻² in 2002
<i>Achillea millefolium</i>	9	17
<i>Arabis hoelboelii</i>	9	0
<i>Arenaria serpyllifolia</i>	62	26
<i>Astragalus purshii</i>	9	0
<i>Bromus tectorum</i>	832	1223
<i>Centaurea diffusa</i>	6945	7147
<i>Collinsia parviflora</i>	0	245
<i>Delphinium bicolor</i>	18	35
<i>Gypsophila paniculatum</i>	1053	1276
<i>Lewisia rediviva</i>	0	9
<i>Linaria dalmatica</i>	88	262
<i>Microsteris gracilis</i>	327	122
<i>Myosotis arvensis</i>	0	26
<i>Myosotis stricta</i>	318	0
<i>Phacelia linearis</i>	9	0
<i>Plantago patagonica</i>	522	926
<i>Polemonium micranthum</i>	318	507
<i>Polygonum douglasii</i>	2875	6361
<i>Potentilla recta</i>	0	44
<i>Pseudoroegneria spicata</i>	53	253
<i>Purshia tridentata</i>	44	166
<i>Rumex acetosella</i>	257	87
<i>Setaria viridis</i>	0	17
<i>Sporobolus cryptandrus</i>	32176	47803
<i>Verbascum thapsus</i>	9	52
<i>Verbena bracteosa</i>	2796	4115
<i>Vicia americana</i>	0	17
<i>Zygadenus venenosus</i>	9	149

Table 3. Mean densities per m² for the 28 vascular plant seeds identified in the seed bank in the 10 x 10 m plots across all treatments at the Osoyoos Desert Centre site in 1999 and 2002.

4.1 Restoration treatment results by treatment

The results of the restoration treatments revealed some major changes in the plant community over the five year period, both in terms of the above-ground cover (Atwood & Scudder, 2003) and in terms of the seed banks among the six restoration treatments.

4.1.1 Solarization

In terms of above-ground vegetation, five weed species were recorded in the solarization plots in 1998 prior to the treatment. In June 2000, two months after the plastic was removed three of the species as well as two new weeds were found in the plots. The average cover of *C. diffusa*, and *Verbascum thapsus* (mullein) was greatly reduced from the 1998 level, but it was evident from the above-ground vegetation growth and seed banks (Fig. 4) that solarization had not killed the seeds. *Bromus tectorum* (cheatgrass) was the third species evident in the plots in June 2000, however seed from it and two new weed species that were found, *Melilotus alba* (sweet white clover) and *Sisymbrium loeselii* (Loesel’s tumble= mustard), likely moved into the plots between April and June. *Agropyron cristatum* (crested wheatgrass) and *Tragopogon dubius* (yellow salsify) were recorded in the solarization plots in 1998 but were not evident in 2000.

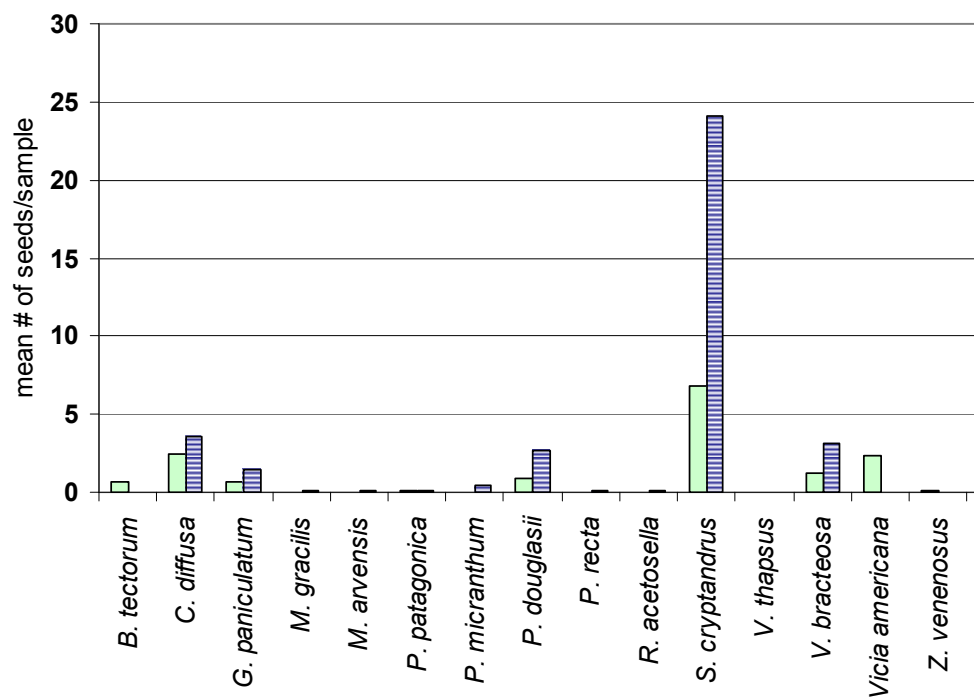


Fig. 4. Mean seed bank composition of solarization plots at the Osoyoos Desert Centre, comparing 1999 seed banks (solid bars) to 2002 seed banks (hatched bars); for full species names see Table 3

Seed bank analysis also indicated that seeds of many plant species were present both after one year of the treatment (1999) and after the solarization treatment in 2002 (Fig. 4). The same four species that dominated the seed bank throughout all plots were dominant in the solarization plots: *S. cryptandrus*, *C. diffusa*, *P. douglassii* and *V. bracteosa*. Interestingly all four species increased between 1999 and 2002 despite the solarization treatment, with *S. cryptandrus* exhibiting an increase from a mean of 7 seeds per sample to 24 seeds per sample. As was the case in the above-ground vegetation the invasive alien species *C. diffusa* and *B. tectorum* were present in the plots after the plastic was installed in 1999, although only *C. diffusa* seeds were found in 2002 samples.

Germination tests done on seeds of *B. tectorum*, *C. diffusa*, and *S. cryptandrus* revealed that some of the seeds were clearly viable despite the extremely high temperatures experienced under the plastic (Fig. 5). In fact, the pattern of germination among the three species, with *S. cryptandrus* exhibiting >40% germination, and *C. diffusa* and *B. tectorum* exhibiting much lower germination percentages was consistent with the pattern seen in all restoration treatments.

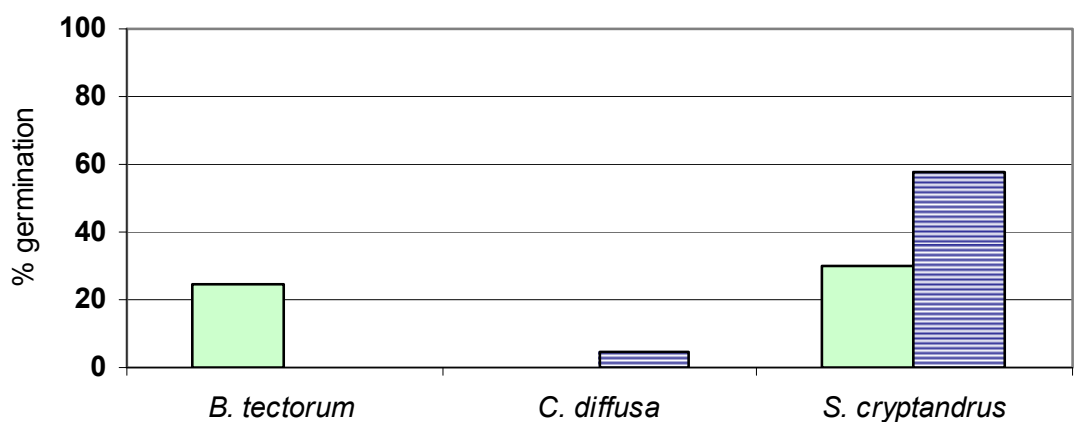


Fig. 5. Percent germination of seeds of three species (*Bromus tectorum*, *Centaurea diffusa* and *Sporobolus cryptandrus*) from the soil under solarization treatments at the Osoyoos Desert Centre site in 1999 (solid bars) and 2002 (hatched bars)

4.1.2 Native bunchgrass hayseeding

The hayseed material added new species to the hayseed plots. *Pseudoroegneria spicata* was not recorded in the hayseed plots in 1998 but in 2002 *P. spicata* accounted for about 1% of the cover. *Hesperostipa comata* was also newly recorded in Replicate 5 hayseed plots in 2002 where *H. comata* cover averaged of $9.0\% \pm 5.5\%$ but its cover did not increase in Replicates 1-4. The hayseed material did not significantly increase the percent cover of *S. cryptandrus*, and the seed bank comparison between 1999 and 2002 showed an 80% decline in mean number of seeds of *S. cryptandrus* per sample.

4.1.3 Removal of livestock grazing (controls)

The removal of livestock had a marked effect on vegetation components across the site. Although there was no change in the average cover of shrubs during the five years, herb and native grass cover increased significantly ($P < 0.05$) and non-native (weed) cover decreased significantly ($P < 0.05$).

The largest reduction in weed cover occurred between 1998 and 1999, the year following the removal of cattle. Weed cover dropped 71% in Replicates 1 to 4 and 77% in Replicate 5 over the four years. *Centaurea diffusa* was the dominant weed on site in 1998 but in 2002, *Agropyron cristatum* (crested wheatgrass), which had been seeded by the former lessee, was the dominant non-native species. In terms of seed banks, small increases were seen in the native species *S. cryptandrus* but also in non-native species such as *C. diffusa* (Fig. 6).

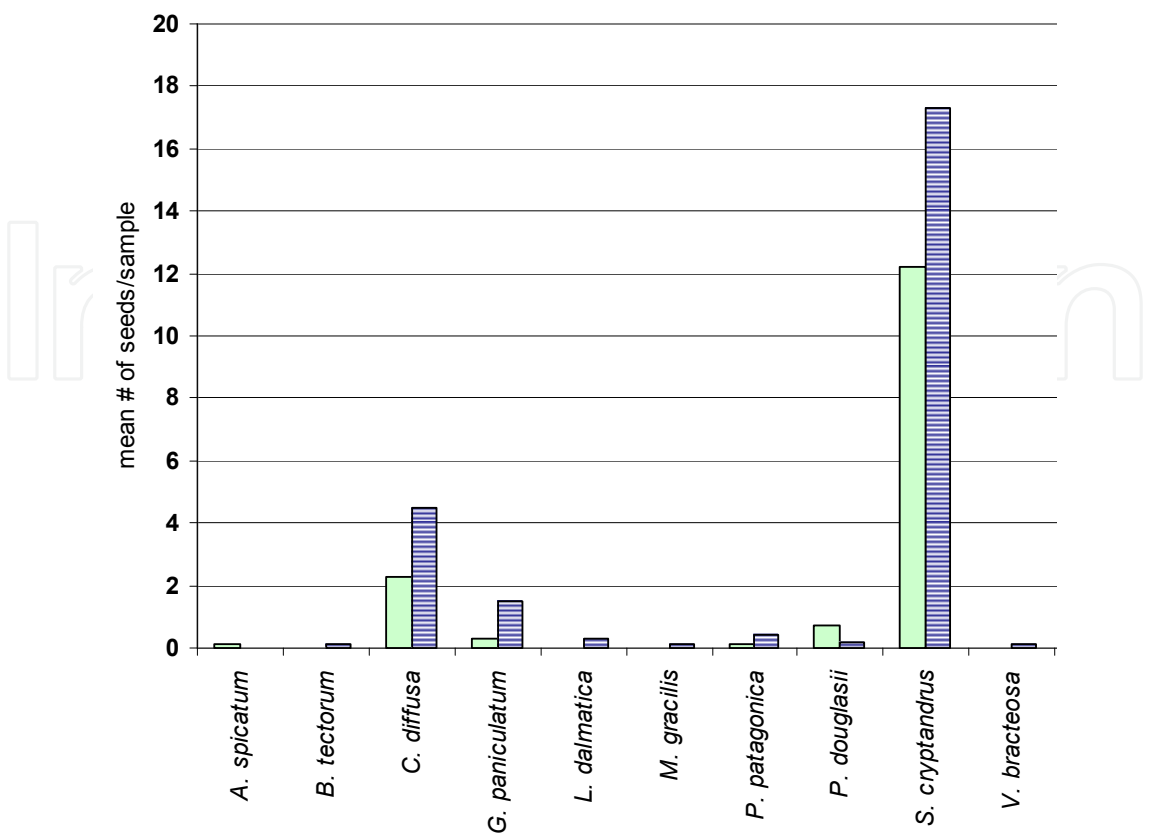


Fig. 6. Mean seed bank composition of control plots at the Osoyoos Desert Centre, comparing 1999 seed banks (solid bars) to 2002 seed banks (hatched bars); for full species names see Table 3; note *A. spicatum* = *P. spicata*

4.1.4 Manual and chemical control of *Centaurea diffusa*

The May 1999 hand weeding (manual treatment) of *C. diffusa* drastically reduced the average cover in the plots between 1999 and 2002 and there was a significant difference in the average cover between the manual treatment plots and control plots (no-treatment) in 1999 and 2000 as a result of the one hand weeding in May 1999 ($P < 0.05$). However, *C. diffusa* was decreasing across the site and by 2001 there was no difference in the cover of *C. diffusa* between the plots that received treatment and those that did not. There was an average of 2.5 *C. diffusa* seeds per sample in the manual removal plots in 1999; the *C. diffusa* seed bank persisted through to 2002 at the same level.

Chemical control with Killex reduced *C. diffusa* cover from an average of $30.33\% \pm 2.74\%$ in 2000 to $0.33\% \pm 0.21\%$ in 2001. However, in 2001 there was no difference in the average cover of *C. diffusa* between plots treated with Killex and control plots ($P > 0.05$). Over the five years of the methods research project, *C. diffusa* decreased rapidly across the site. Over the long-term, the control plots (i.e., merely removing livestock) showed the same level of decline as the plots where *C. diffusa* was treated. Gayton (2011) showed that the period from 1998-2002 was the beginning of a long-term decline in populations of *C. diffusa* on the site due to predation by several insects introduced to the region to provide biological control, resulting in virtually zero percent cover on the site by 2009.

4.1.5 Addition of native vesicular arbuscular mycorrhizae and native seed

Although initially very little difference was seen due to the addition of native vesicular mycorrhizae, by 2001, there was a significantly higher average cover of *P. spicata* in the plots inoculated with VAM and this relationship was still evident in 2002. Cover of the native grasses did not change significantly between 2001 and 2002 except for *H. comata*, which more than doubled in this one year. The seed bank of *S. cryptandrus* in these plots increased three-fold between 1999 and 2002, but the 2002 level was just 12 seeds per sample.

4.1.6 Addition of native seed

Significantly greater cover of native grasses occurred in no-till versus tilled seedbed preparation ($P < 0.05$). After one growing season, cover of seeded grasses in tilled plots averaged $9.13\% \pm 1.59$ compared to $26.57\% \pm 2.99$ in no-till plots.

After one growing season there were significant differences in the percent cover of the native grass seedlings, but it differed by species. There was little response in % cover by *P. spicata* or *S. cryptandrus* but *A. longiseta* and *H. comata* responded differently in the different replications; *S. cryptandrus* did tend to exhibit moderate increases from 1999 to 2002 in the seed bank in all seeding treatments. The average cover of *A. longiseta* was significantly higher in the sandy soils of Replicate 5 ($P < 0.05$) and the average cover of *H. comata* was significantly higher in Replicates 1 to 4, which contained soils with a higher silt content ($P < 0.05$).

4.2 Overall restoration treatment results

On the Osoyoos Desert Centre research site, locally collected natural grasses established successfully as a result of both hayseeding and broadcast seeding. Broadcast seeding was more effective than hayseeding on undisturbed soils and seeding rate (1027 seeds per m^2 versus 1504 seeds per m^2) did not affect establishment. Further work is required to determine if the level of plant establishment is a reflection of the carrying capacity of the local soils, given their low moisture and nutrient availability (Wicklow, 1994) or the result of self-induced seed dormancy, which has limited germination in harsh environmental conditions (Halvorson & Lang, 1989; Allen et al., 1994; O'Keefe, 1996).

The hayseed appeared to repress one of the most common native grasses on the site, *S. cryptandrus*. The average cover of *S. cryptandrus* fell slightly in Replicates 1-4 over the four years as compared to an 18% increase in cover in the control plots. The cover of *S. cryptandrus* did not decrease in Replicate 5 where light availability was likely higher, even with the hayseed cover. Sabo et al. (1979) reported germination of *S. cryptandrus* increased with light availability. In contrast, the hayseed cover enhanced *P. spicata* and *H. comata* establishment. *Pseudoroegneria spicata*, absent from the research plots before seeding, only established in areas that received the hayseed mulch or vesicular arbuscular mycorrhizae (VAM) inoculant. All of the seeded grasses are mycorrhizal (Trappe, 1981) and VAM is particularly critical for the establishment of warm season grasses (Clapperton & Ryan, 2001), which would include *A. longiseta* and *S. cryptandrus*. To date, VAM colonization levels that will improve grass establishment are unknown.

Species establishment was also influenced by soil type. *Aristida longiseta* had higher establishment in sandier soils, while *H. comata* did best in siltier soils. Both species are promoted as drought tolerant species and yet the limited establishment of *A. longiseta* and restricted conditions favouring establishment of *H. comata* suggests that they were affected by dry conditions experienced in the South Okanagan during the interval of the study. Weaver (1968) found that *A. longiseta* decreased during extended droughts.

Solarization was not an effective weed control method for the primary weeds on the Osoyoos Desert site. *Centaurea diffusa* and *V. thapsus* germinated readily following the removal of the plastic, indicating the 75 C recorded under the plastic during treatment was not sufficient to kill the seeds (see also section 5). In addition, solarization resembles broadcast herbicide treatment, exposing large expanses of bare soil after treatment. Revegetating solarized areas with native species will also require a consistent and long-term weed control program.

Manual and chemical control of *C. diffusa* did reduce the weed component, however results were confounded by biological control agents, which were also onsite. In one-year weed cover in the plots monitored for the effect of the removal of livestock declined by about 75% and over five years there was a significant increase in native grass and herb cover. The rapid decline of *C. diffusa* was puzzling since the species is known to have an extensive and long-lived seed bank. Reduced soil disturbance is a factor, because *C. diffusa* did germinate in the tilled plots. The presence of few viable knapweed seeds on the site may be indicative of the successful result of *Sphenoptera jugoslavica* (a beetle utilized as a biological control agent), which occurs throughout the area. Similarly, throughout the region major declines in *C. diffusa* due to success of biological agents have been observed (Myers et al., 2009; Gayton, 2011). By 2002, *A. cristatum* was the dominant non-native species on the site.

5. Solarization and high temperature exposure

As well as the indications from both above-ground cover and seed bank sampling of the solarization plots, experimental exposure of seeds of *C. diffusa* and *S. crypanthus* to temperatures even higher than solarization temperatures served to confirm that seeds of both species are highly resilient to high temperatures.

5.1 Solarization and high temperature impacts on seeds of *Centaurea diffusa*

Fewer diffuse knapweed seeds per sample occurred in the non-solarization samples than in the solarization samples ($P < 0.05$, student's t-test). There were 0.98 ± 1.1 SD and 2.2 ± 2.6 SD diffuse knapweed seeds per sample, in non-solarization and solarization samples, respectively. This amounted to a total of 71 seeds in the solarization plots and 39 seeds in the non-solarization plots. Three seeds from non-solarization plots and one seed from the solarization plots germinated. No other non-solarization plot seeds were found viable by the tetrazolium test, while 2 additional seeds from solarization plots were evaluated as viable. There was no difference ($P < 0.05$) between mean viability of seeds per sample, which was 0.10 ± 0.31 SD and 0.06 ± 0.24 SD seeds per sample for solarization and non-solarization plots, respectively. The relatively low viability of diffuse knapweed seeds of 4% within solarization plots is similar to a value of 3% recorded in another study of seed banks in the southern Okanagan (Clements et al., 2007). Germination and viability tests

indicate it is possible for diffuse knapweed seeds to remain viable despite exposure within solarization treatments to temperatures frequently ranging over 40 C with peaks greater than 70 C.

Germination did not differ with the length of the heat shock treatment, although there were differences in the percent of germination between wet and dry seeds (Table 4). There were no differences among seeds exposed to 40 C, whether wet or dry with all treatments exhibiting germination of 60% or higher. Non-heat shocked control germination percentages ranged from 40-70%. Germination was significantly reduced to less than 15% for wet seeds exposed to 50 C and no germination was observed for wet seeds exposed to temperatures of 60 C and higher. By contrast, dry seeds germinated following exposure of temperatures up to 90 C, although the germination percentage was significantly reduced. The germination percentage for dry seeds progressively declined with increasing temperatures. Germination of 21 ± 29 SD % and 18 ± 25 SD % was recorded after 1-h and 5-h exposures of dry seeds to 90 C, respectively. No germination of dry seeds was observed following exposure to 100 C, and the seed embryos exhibited a liquefied appearance.

Temperature (C)	5 h wet	1 h wet	5 h dry	1 h dry
40	60 (24) Aa	80 (13) Aa	83 (16) Aa	76 (23) Aab
50	12 (16) Bb	13 (28) Bb	52 (31) Aab	71 (34) Aabc
60	0 (0) Bb	0 (0) Bb	69 (28) Aab	90 (12) Aa
70	0 (0) Bb	0 (0) Bb	56 (38) Aab	56 (15) Abc
80	0 (0) Bb	0 (0) Bb	42 (23) Abc	44 (38) Acd
90	0 (0) Ab	0 (0) Ab	18 (25) Acd	21 (29) Ade
100	0 (0) Ab	0 (0) Ab	0 (0) Ad	0 (0) Ae

Table 4. Mean % germination (± standard deviation) for *Centaurea diffusa* seeds heat shocked for either 1 h or 5 h at various temperatures; means within a row followed by the same upper case letter are not significantly different at the 5% level; means within a column followed by the same lower case letter are not significantly different at the 5% level (Fisher's Protected LSD test)

Although no seeds incubated in a moist environment germinated above 50 C, the tetrazolium test indicated that some seeds were viable after exposure to higher temperatures, although percent viability was significantly lower for these treatments than for the dry incubated seeds (Table 5). Even after exposure to 90 C, seed viability of 2 ± 5 SD % and 12 ± 13 SD % was recorded in the 5-h wet and 1-h wet heat shock treatments, respectively. Viability was reduced at 60 C or higher, with less than 30 % of wet seeds exposed to temperatures of 60 C still viable. Within the dry heat shock treatments, viability was generally >90%, up to and including 80 C. Viability of dry incubated seeds was significantly reduced for 90 C heat shock treatments compared to lower temperatures, but still remained substantial at 38 ± 43 SD % and 54 ± 29 SD % for 1-h and 5-h exposures of dry seeds, respectively. Though the tetrazolium test does not predict

seed viability with complete reliability, the indication that even more seeds were likely capable of germinating than actually germinated further supports the likelihood of large numbers of diffuse knapweed seeds surviving solarization treatments. Whether or not sub-lethal high temperatures actually induced seed dormancy, as was the case for *Sida spinosa*, *Amaranthus retroflexus*, *Abutilon theophrasti*, *Anoda cristata*, and *Ipomoea lacunosa* (Egley, 1990) cannot be inferred from the data recorded in this study, nor is it known whether high temperatures induce dormancy in diffuse knapweed seeds. As seen in other species, it is possible that temperatures of 50-60 C may break dormancy in some seeds, possibly stimulating germination and subsequently mortality of emerging seedlings (Rubin & Benjamin, 1984).

Temperature (C)	5 h wet	1 h wet	5 h dry	1 h dry
40	85 (20) Aa	96 (9) Aa	98 (5) Aa	96 (9) Aa
50	42 (48) Bb	66 (38) ABb	96 (9) Aa	94 (9) Aa
60	2 (5) Bc	6 (9) Bc	98 (5) Aa	96 (9) Aa
70	28 (24) Bbc	22 (33) Bc	98 (5) Aa	90 (17) Aa
80	22 (29) Bbc	10 (12) Bc	86 (22) Aa	96 (9) Aa
90	2 (5) Cc	12 (13) BCc	54 (29) Ab	38 (43) ABb

Table 5. Mean % viability (\pm standard deviation) for *Centaurea diffusa* seeds heat shocked for either 1 h or 5 h at various temperatures; percent viability includes seeds germinating under optimal conditions and seeds that were viable according to the tetrazolium test; means within a row followed by the same upper case letter are not significantly different at the 5% level; means within a column followed by the same lower case letter are not significantly different at the 5% level (Fisher's Protected LSD test)

The 1-h and 5-h *in vitro* tests in the current study only examined the effect of a single exposure to high temperatures. It is not known whether long-term temperature fluctuations over the season would increase mortality of diffuse knapweed seeds due to exposure to high temperatures. It is also unclear what effect condensation on the soil surface beneath the plastic has on seed germination and viability. Studies where seeds of other species were incubated at high temperatures over longer periods of time (i.e., one week or more) also recorded high survival rates of seeds (Horowitz et al., 1983; Egley, 1990). Although Horowitz et al. (1983) found that 2-4 wks of solarization provided control of many annual weed species, there were still some seeds that retained viability after 8 wks.

5.2 Solarization and high temperature impacts on seeds of *Sporobolus cryptandrus*

As shown in Fig. 5, seeds of *S. cryptandrus* maintained relatively high germination percentages even when exposed to the relatively high temperatures experienced in solarization treatments, with *S. cryptandrus* seeds from solarization treatments in 1999 exhibiting 30% germination, and *S. cryptandrus* seeds in 2002 exhibiting 58% germination. In the control treatments, *S. cryptandrus* seeds exhibited 10% and 33% germination in 1999 and

2002 respectively; in the hayseeding experiments *S. cryptandrus* seeds exhibited 34 and 66% germination, respectively.

As in the case of *C. diffusa*, seeds of *S. cryptandrus* maintained a high level of viability, when heat shocked at temperatures experienced under solarization (i.e., 70 C) and at even higher temperatures (110 C). Of the 82 seeds of *S. cryptandrus* we heat shocked at 70 C, 32% were viable; of the 45 seeds of *S. cryptandrus* we heat shocked at 110 C, 16% were viable. Unlike the *C. diffusa* seeds that were heat shocked which were collected the previous fall from seed heads on the plants, the source of seeds for the *S. cryptandrus* heat shock trials was seeds extracted from the soil at the Osoyoos Desert site. Thus, the moderate level of viability at 70 C and yet substantial viability at 110 C was observed despite other factors that already would have lead to decline in seed viability in the soil environment prior to heat shocking.

6. Implications for restoration of ecosystems

6.1 Solarization as a means of managing invasive species

The temperatures experienced under the polyethylene under field conditions were extremely high, even by comparison to other locations, such as Mississippi, where 70 C is unlikely to be observed on a frequent basis (Egley, 1983). The survival of viable *C. diffusa* seeds under these conditions, and after heat-shock treatments of even higher temperatures under laboratory conditions renders the elimination of the *C. diffusa* seed bank by solarization unlikely. It should also be considered that some *C. diffusa* seeds may be located deep enough within the soil profile to avoid the extreme temperatures at the soil surface (Rubin and Benjamin 1984; Standifer et al., 1984). Standifer et al. (1984) found seed mortality due to solarization decreased with depth in the soil, and was primarily effective in the top 5 cm. As observed elsewhere, solarization would reduce the seed bank population to some degree while exhibiting its primary impact on above-ground plants (Horowitz et al., 1983; Egley, 1990). Furthermore, solarization may have limited impact on perennial or biennial species, whose growth may actually be stimulated by solarization (Stapleton & DeVay, 1986; Sauerborn et al., 1989; Linke, 1994). Given that *C. diffusa* is a biennial or short-lived perennial, it would be interesting to investigate the effect of solarization on its perennating tissues.

The long-term ramifications of the small reduction in seed viability of *C. diffusa*, following a short-term exposure to excessive temperatures, on plant community dynamics are unclear. Without re-seeding native plant species, *C. diffusa* could re-establish from the seed bank and nearby seed sources, particularly in the wake of the disturbance caused by the removal of above-ground vegetation by solarization. With sufficient re-seeding of desired plant species, the impact of emerging *C. diffusa* seedlings may be minimal, particularly in light of the relatively low percentage of *C. diffusa* seeds that remain viable in the seed bank (Clements et al., 2007). The scale of solarization treatments is also a critical issue. The efficiency of solarization in minimizing weed interference has been demonstrated in horticultural crops (Braun et al., 1988; Horowitz et al., 1983; Jacobsohn et al., 1980; Linke, 1994). However, restoring large areas of natural habitat is more difficult, particularly in the face of disturbance-adapted weeds like *C. diffusa* that are abundant over large areas and possess persistent seed banks resilient to high temperatures. Solarization is an efficient weed control

technique in horticultural crops (Jacobsohn et al. 1980; Horowitz et al. 1983; Braun et al. 1988; Linke 1994) and may be an inexpensive and labour-saving tool for reducing weeds in natural habitats protected from chemical treatments or disturbed soils where weeds dominate. This study suggests solarization will not control diffuse knapweed in the South Okanagan, however many issues require further study.

6.2 Recommendations for managing shrub-steppe ecosystems incorporating knowledge of seed bank dynamics

The importance of removing or at least reducing disturbance by livestock was clear from this study as even apart from other restoration measures, livestock removal was effective in increasing the native species component in these shrub-steppe plant communities. Likewise in a study of 10 sites with varying grazing regimes in the same region of the southern Okanagan valley, Krannitz (2008) found that more bare soil was associated with livestock grazing, with particularly large impacts seen in sandy versus rocky sites, and in areas not protected by antelope brush shrubs. The presence of bare soil meant that there was a corresponding loss in microbiotic crust cover, and this meant reduced overall health of the native plant community primarily due to lack of moisture retention without crust (Atwood & Krannitz, 2000; Krannitz, 2008).

Another mechanism by which differences in microbiotic crust may impact plant communities is through variations in seed bank dynamics depending on degree of crust cover. Crust cover is predicted to affect seed burial and longevity of the seeds; in soil samples with a large portion of the crust constituents (i.e., lichens and mosses), seeds in our samples were often located among the microbiotic vegetation, hence relatively close to the soil surface. In general, seed survival nearer to the surface is reduced (Harper, 1977; Clements et al., 1996), but it is probable that seeds falling among microbiotic crust would be preserved longer than seeds occurring on the soil surface (Langhans et al., 2010). Seed bank studies in the southern Okanagan point to the need for more research in this area to enable ecosystem managers to fine-tune approaches to grazing levels, restoration plantings, and management of fire and other disturbances (Krannitz & Mottishaw, 2004; Clements et al., 2007).

Few studies have investigated the relationship of seed bank dynamics to microbiotic crusts experimentally, and many of the few studies that have been done under laboratory conditions, therefore not matching conditions of normal seed dispersal (Prasse & Bornkamm, 2000; Su et al., 2007). A study in the north-western Negev desert of Israel found that increased roughness of the surface due to the presence of crust reduced the probability of seeds coming to rest, therefore lowered seed emergence and survival (Prasse & Bornkamm, 2000). However, other have found increased seed bank emergence with increased crust presence (Su et al., 2007). A study in the Teng-ger Desert in northeastern China observed much greater vascular plant emergence with moss crusts than algae crusts, with seeds more likely to become lodged in the moss crusts, even under high wind conditions (Su et al., 2007). Water status was also a major factor in the Chinese study, as it was in a study of crust types in Idaho within the Great Basin of North America (Serpe et al., 2006), with more moisture producing greater seedling emergence. Serpe et al. (2006) also pointed out that seedling emergence responses can vary with specific crust structure; different seed and seedling morphotypes likewise have a major influence on the result. Thus

while studies from other regions provide some basis for understanding relationships between soil crusts and recruitment of vascular plants from the seed bank, there is a need for experimental studies within specific regions in order to know how best to restore semi-arid steppe grasslands after crust degradation.

In our study broadcast seeding was more effective than hayseeding on undisturbed soils and seed rate did not affect establishment. Rates of greater than 1000 seeds per m² are thought to be high (Jacobs et al., 1999) and it appears applications that exceed that amount are unnecessary. The apparent repression by the hayseed of the most common grass species on the site, *S. cryptandrus*, may represent be an important management consideration if *S. cryptandrus* is considered a valuable component of the community, as a major constituent of the native seed bank. Strategically developing restoration management to encompass disturbance-adapted native species such as *S. cryptandrus* may be difficult.

In contrast, the hayseed cover did enhance other native grass species such as *P. spicata* and *H. comata* establishment, and likewise vascular arbuscular mycorrhizal inoculant was very helpful to the establishment of some of the native grasses as has been seen in other studies (Camill et al., 2004; Anderson, 2008). It would be interesting to explore the connections between health of the microbiotic crust and the vigour of vascular arbuscular mycorrhizae in this system.

In addition to its ineffectiveness in terms of destroying weed seeds, the result of solarization resembled that of applying broadcast herbicides because large expanses of bare soil were exposed after treatment. Manual and chemical control of *C. diffusa* did reduce weed biomass, but ultimately populations decreased with the removal of livestock removal coupled with the cumulative success of biological control. The populations of insects utilized in biological control of *C. diffusa* have increased enough to reduce the populations of *C. diffusa* to negligible levels at this site and many others in the region, even with the persistent seed bank of this species (Myers et al., 2009; Gayton, 2011).

Based on the preceding discussion and results, we can make the following recommendations for restoration of communities within these arid shrub-steppe ecosystems:

- Restoration measures should minimize soil disturbance
- Measures to restore a diverse and healthy native plant community must include the microbiotic crust in these ecosystems
- Livestock grazing must be monitored rigorously to limit unnecessary soil disturbance
- Restoration planting, particularly if involving warm-season grasses, may be enhanced by incorporation of vesicular arbuscular mycorrhizae
- Restoration planting and invasive species control should account for native species with seed banks such as *Sporobolus cryptandrus*
- Spatial dispersion and amount of shrub cover should be carefully managed to promote native plants and reduce influence of grazing and non-native plants
- Long-term planning should be developed to monitor ecosystem conditions, invasive species, and other important management factors such as biological control as well as the desired ecosystem trajectory



Fig. 7. Kiosk at the Osoyoos Desert Society site showing amidst the grassland ecosystem with scattered shrubs of antelope bitterbrush (*Purshia tridentata*); photo courtesy of the Osoyoos Desert Society

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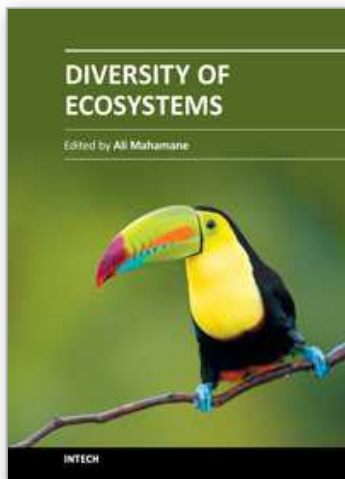
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The ecosystems present a great diversity worldwide and use various functionalities according to ecologic regions. In this new context of variability and climatic changes, these ecosystems undergo notable modifications amplified by domestic uses of which it was subjected to. Indeed the ecosystems render diverse services to humanity from their composition and structure but the tolerable levels are unknown. The preservation of these ecosystemic services needs a clear understanding of their complexity. The role of research is not only to characterise the ecosystems but also to clearly define the tolerable usage levels. Their characterisation proves to be important not only for the local populations that use it but also for the conservation of biodiversity. Hence, the measurement, management and protection of ecosystems need innovative and diverse methods. For all these reasons, the aim of this book is to bring out a general view on the function of ecosystems, modelling, sampling strategies, invading species, the response of organisms to modifications, the carbon dynamics, the mathematical models and theories that can be applied in diverse conditions.

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University Campus STeP Ri
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51000 Rijeka, Croatia
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Unit 405, Office Block, Hotel Equatorial Shanghai
No.65, Yan An Road (West), Shanghai, 200040, China
中国上海市延安西路65号上海国际贵都大饭店办公楼405单元
Phone: +86-21-62489820
Fax: +86-21-62489821

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